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Theta oscillations promote temporal sequence learning

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ABSTRACT

Many theoretical models suggest that neural oscillations play a role in learning or retrieval of temporal sequences, but the extent to which oscillations support sequence representation remains unclear. To address this question, we used scalp electroencephalography (EEG) to examine oscillatory activity over learning of different object sequences. Participants made semantic decisions on each object as they were presented in a continuous stream. For three "Consistent" sequences, the order of the objects was always fixed. Activity during Consistent sequences was compared to "Random" sequences that consisted of the same objects presented in a different order on each repetition. Over the course of learning, participants made faster semantic decisions to objects in Consistent, as compared to objects in Random sequences. Thus, participants were able to use sequence knowledge to predict upcoming items in Consistent sequences. EEG analyses revealed decreased oscillatory power in the theta (4–7 Hz) band at frontal sites following decisions about objects in Consistent sequences, as compared with objects in Random sequences. The theta power difference between Consistent and Random only emerged in the second half of the task, as participants were more effectively able to predict items in Consistent sequences. Moreover, we found increases in parieto-occipital alpha (10–13 Hz) and beta (14–28 Hz) power during the pre-response period for objects in Consistent sequences, relative to objects in Random sequences. Linear mixed effects modeling revealed that single trial theta oscillations were related to reaction time for future objects in a sequence, whereas beta and alpha oscillations were only predictive of reaction time on the current trial. These results indicate that theta and alpha/beta activity preferentially relate to future and current events, respectively. More generally our findings highlight the importance of band-specific neural oscillations in the learning of temporal order information.

1. Introduction

Episodic memories can be conceptualized as temporally-organized sequences of events (Allen & Fortin, 2013). Computational models suggest that neural oscillations—rhythmic fluctuations in the excitability of large neuronal populations—might play a role in the coding of temporal sequences (Lisman & Idiart, 1995; Lisman & Jensen, 2013). In humans, oscillatory power in the theta band (4–7 Hz) is readily observable in scalp electroencephalography (EEG), magnetoencephalography (MEG), and intracranial recordings. Available evidence indicates that theta oscillations may be generated by a network that includes the hippocampus, medial prefrontal cortex, and medial/lateral parietal cortex (see Hsieh & Ranganath, 2014, for review). Critically, neuroimaging studies have implicated these regions in encoding (e.g. Ekstrom & Bookheimer, 2007; Jenkins & Ranganath, 2010; Tubridy & Davachi, 2011) and representation (Hsieh and Ranganath, 2015; Hsieh, Gruber, Jenkins, & Ranganath, 2014; Kalm, Davis, & Norris, 2013) of event sequences.

Scalp EEG studies have provided evidence that theta power is critical for successful episodic encoding and retrieval (Fuentemilla, Barnes, Düzel, & Levine, 2014; Long, Burke, & Kahana, 2014; Rozengurt, Barnea, Uchida, & Levy, 2016; Sederberg, Kahana, Howard, Donner, & Madsen, 2003). Available evidence also suggests that theta activity might contribute to sequence processing (e.g., Heusser, Poeppel, Ezzyat, & Davachi, 2016; Hsieh et al., 2011; Roberts et al., 2013). For instance, EEG studies of working memory (Hsieh et al., 2011; Roberts et al., 2013) have shown that theta power is higher during active maintenance of temporal order information than during maintenance of detailed object information. These findings indicate that theta power could reflect online maintenance of temporal order relationships. Some evidence, however, suggests an alternate possibility—that theta activity could reflect prediction errors. Indeed,

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numerous studies have found that theta power is increased following erroneous responses, and the evidence indicates that these increases reflect feedback or error-driven learning (Cavanagh & Frank, 2014; Cavanagh et al., 2012; Cavanagh, Frank, Klein, & Allen, 2009, 2010; Cohen, 2011; Cohen, Elger, & Ranganath, 2007). Recordings from non-human primates (Brincat & Miller, 2015) have also provided support for the importance of theta oscillations in error-driven learning, showing increased oscillatory synchrony in the theta band between hippocampus and prefrontal cortex following errors that decrease as a function of learning. Thus, it is possible that theta oscillations would be most prominent as participants are learning sequence information (i.e., when prediction error is high), and that it should decline as one learns to use sequence knowledge to predict upcoming events (see Clarke et al., 2017).

To examine the extent to which theta oscillations support sequence learning or representation, we used scalp electroencephalography (EEG) to record oscillatory activity as participants performed a sequence-learning task. EEG was recorded as participants made simple semantic judgments on a stream of consecutively presented objects, consisting of sequences of objects that were presented in the same order on each repetition ("Consistent") and sequences of objects that appeared in a different order on each repetition ("Random"). Because objects in Consistent and Random sequences were equally familiar, comparison of the two conditions allowed us to investigate learning of temporal relationships that enabled prediction of upcoming objects in Consistent sequences. To investigate the role of oscillatory activity during learning of structured order information, we directly contrasted activity between Consistent and Random sequences over the course of learning. We characterized the timing and functional characteristics of activity in the theta, alpha, and beta bands, thereby allowing us to identify whether any learning-related effects were band-specific.

2. Materials and Methods

2.1. Participants

Twenty healthy (6 males) undergraduate students from the University of California at Davis were included in this study. All participants had normal or corrected-to-normal vision. The Institutional Review Board at the University of California at Davis approved the study. Written informed consent was obtained from each subject before the experiment.

2.2. Task procedures

Task procedures were modified from Hsieh et al. (2014). The current study consisted of two parts: a sequence learning session and a sequence retrieval session. EEG data were only acquired during the sequence learning session. Therefore, EEG analyses and results reported in this paper focus on the sequence-learning portion of the experiment. The learning session consisted of four study-test blocks. During the study phase of each block, participants were presented with a stream of objects, each presented for 1000 ms, and separated by a 1500 ms fixation cross. The stream consisted of repetitions of six different five-object sequences. The Fixed sequence consisted of five distinct objects, presented in the same order on each repetition. Objects in the Fixed sequence did not overlap with objects in other sequences (see Fig. 2A). Two overlapping sequences ("X1" and "X2") also consisted of five objects presented in the same order on each repetition, but unlike the Fixed sequence, X1 and X2 sequences shared common objects in positions 2 and 3 (see Fig. 2A). Two Random sequences that each consisted of five distinct objects, presented in a different pseudorandom order on each repetition. As a result, participants could not learn a consistent temporal relationship between objects in the Random sequences. Lastly, a "Novel" sequence was presented, consisting of trial-unique objects that were only presented once in the entire experiment. In other words, a completely new set of five objects was presented on every repetition of the Novel sequence. Novel sequences were not included in the analyses reported here, as this manuscript is focused on changes in EEG oscillations over the course of sequence learning, rather than item learning.

Each object sequence was presented six times during the study phase of each study-test block, with the constraints that: (1) there were no back-to-back repetitions of the same sequence type, and (2) all object sequences must have been presented before subsequent repetitions. To keep participants actively engaged and obtain behavioral measures of sequence learning, participants were required to make a semantic decision to each presented object in the continuous object stream, based on a semantic question (e.g. "Is the presented object living?") provided at the beginning of the study phase of each study-test block. A different semantic question was used in different study-test blocks. Because the sequences were presented contiguously, there were no obvious divisions between different object sequences. However, participants were instructed to look out for, and learn, the sequence relationships.

During the test phase of each block, participants were asked to recall each object sequence (except for the Novel sequences). On each self-paced test trial, five objects from a sequence were simultaneously presented in a random order from left to right on the screen. Participants were asked to reconstruct the temporal order in which these objects appeared during the study phase. Participants were additionally instructed that, if there was no consistent temporal order (which was true for objects in the Random sequences), then they were to put the items in any order. After each test trial, the correct order of the objects was presented on the screen. For the Random sequences, the objects were shown in a random order during the feedback period. Each sequence type was tested two times in each test block, with the constraint that: (1) there were no back-to-back tests of a particular sequence type, and (2) each sequence was tested once before any sequence was retested.

2.3. Behavioral analyses

Our primary hypotheses were centered on sequence learning, and we therefore focused on contrasting EEG and behavioral data between the Consistent sequences (collapsed across Fixed, X1, and X2 sequences) and the Random sequences. Study blocks were also divided into early (Blocks 1 and 2) and late (Blocks 3 and 4) blocks. ANOVAs were conducted using the AFEX package in R (Singmann et al., 2017). The Greenhouse Geisser Correction (Greenhouse & Geisser, 1959) was applied to account for violations of sphericity where appropriate.

2.4. EEG data acquisition

EEG was recorded from 128 silver/silver chloride electrodes mounted in an elastic cap using an ActiveTwo EEG recording system (Biosemi, https://www.biosemi.com/). The positioning of the 128 electrodes was in accordance with an extended version of the international 10/20 system (Klem, Luders, Jasper, & Elger, 1958; Oostenveld & Praamstra, 2001). Additional electrodes were placed on the mastoids, outside the outer canthi of both eyes, and above and below the left eye. Data were collected at a sampling rate of 2048 Hz.

2.5. EEG Analysis

All data analyses were performed offline using the EEGLab Toolbox (Delorme and Makeig, 2004) and Fieldtrip Toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The continuous EEG data were first high-pass filtered at 0.5 Hz and then down sampled to 512 Hz. Channels with excessive noise due to channel failure were identified and their data were interpolated using spherical interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). Continuous EEG data were then segmented to single trials time-locked to response onsets (−600 ms to

600 ms) to control for differences in response latencies between sequence types. To remove oculomotor artifacts, Independent Component Analysis (ICA) was performed and components associated with eye-blinks and other oculomotor artifacts were identified and removed. EEG epochs then underwent an artifact rejection procedure to remove EEG epochs with extreme values (± 100 micro-volt). Visual inspection was also performed to remove any remaining artifacts that were not captured by artifact rejection. Single-trial EEG epochs were subsequently transformed to current density values using a surface Laplacian transformation (Kayser and Tenke, 2006) with the following parameters: m-constant = 4 and smoothing constant $\lambda = 10^{-6}$. The surface Laplacian transformation was performed because it minimizes volume conduction from deep sources, thereby providing a more sharply localized scalp topography of observed EEG effects (Nunez & Srinivasan, 2006). We then computed EEG spectral power by convolving single-trial EEG epochs from each scalp electrode using 6 cycle complex Morlet wavelets at linearly spaced frequencies between 4 and 50 Hz at 10 ms steps. The spectral data were log transformed then baseline corrected with respect to spectral data in the time window of −800 to −500 relative to stimulus onsets. Time frequency representations (TFRs) were averaged across positions 1–4 and divided into early blocks (Blocks 1 and 2) and late blocks (Blocks 3 and 4) for Consistent and Random sequences separately.

2.6. Frequency clustering

Oscillatory activity recorded at the scalp tends to reliably occur in characteristic frequency bands, particularly in the theta, alpha, and beta bands. To define frequency bands in a data-driven manner, we used a hierarchical clustering analysis procedure. TFRs were averaged across subjects and trials to yield a grand average TFR for each electrode. Data at each frequency were then vectorized and pairwise linear distance (using Pearson's r) was computed between the time courses of individual frequencies and across electrodes. A hierarchical clustering algorithm (UPGMA, Mathworks) was then applied to create a dendrogram that best captured the correlation structure between individual frequencies (Fig. 1). We thresholded the dendrogram such that frequency clusters that closely approximated the canonical frequency bands. Subsequent analyses were based on the identified frequency bands of theta (4–7 Hz), alpha (10–13 Hz), and beta (14–28 Hz), frequencies within the gamma band were not analyzed because these rhythms can be contaminated by muscle and eye movements. (Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008).

2.7. Statistical analyses

Statistical analyses were performed on frequency bands of interest identified by our frequency clustering algorithm (see above) using cluster-based permutation tests implemented in Fieldtrip (Oostenveld et al., 2011), which identified significant spatio-temporal clusters within a given frequency band. This procedure involved a Monte-Carlo randomization procedure, in which trial labels were randomly shuffled for each subject in each permutation and a total of 1000 permutations were performed to control for multiple comparisons (see Maris and Oostenveld, 2007). Conditions-of-interest were contrasted using a two-tailed dependent samples *t*-test. Significant spatio-temporal clusters were defined as electrode-time pairs with at least two other significant neighboring electrodes that exceeded a significance threshold of $\alpha = 0.05$. It is important to note that power analyses on stimulus-locked data produces a similar pattern of results (although the theta effects were only marginally significant; $p = 0.07$).

2.8. Linear mixed effects models

We employed a linear mixed effects model with a maximal random effects structure (Barr et al., 2014) to determine whether reaction time on a given trial could be predicted by the oscillatory activity associated with the previous trial. Reaction time for the current trial was used as the dependent variable, and predictor variables were theta power, beta power, and alpha power on the previous trial, as well as alpha and beta power on the current trial. Alpha and beta power on the current trial were included to evaluate the contributions of these frequency bands on the production of a response and motor preparation on the current trial. Theta power on the current trial was not included in the model because theta effects appeared after the response for a given trial and thus could not be used to predict upcoming reaction time. Subjects and object identity (e.g. Fish, Tractor) were defined as the random factors in the model, which allowed the intercepts to vary for individual participants and object stimuli. Object identity was included as a random factor order to account for stimulus-specific influences on response time (Barr et al., 2014). Random slopes were also included for all predictors. This analysis focused on RTs for trials that occupied serial positions 1 through 4, because participants could not predict which object would come after the fifth object (i.e., the last object) in a sequence. Analysis was further constrained to Consistent (Fixed, X1, and X2) sequences in late blocks, as we expect that the consistent temporal structure in these sequences might reinforce the relationship between reaction time and oscillatory activity and that such relationship would be strongest when participants had learned the sequences, especially in late blocks. Given that the objects in Consistent sequences are highly primed and predictable, participants were able to respond quickly (faster than 400 ms). To ensure that our effects were not driven by these trials we ran the same model described above, but removed trials where subjects were able to respond very quickly and the results were unchanged. Statistical tests on fixed effects were performed using the Kenward-Rogers approximation implemented in the AFEX (Singmann et al., 2017) package in R to obtain accurate p-values.

3. Results

3.1. Behavioral results during sequence learning

Based on our previous work (Hsieh et al., 2014), we predicted that, as the learning phase progressed, participants would be able to use their acquired sequence knowledge to facilitate semantic decisions for objects in sequences that followed a consistent order (i.e., the Fixed, X1, and X2 sequences), relative to objects in the Random sequences. We predicted that, in early blocks, all sequence types would have similar reaction times. If participants were able to learn and use sequence relationships to facilitate their semantic decision, then we would expect RTs in late blocks to be faster for positions 2–5 in the Fixed, X1, and X2 sequences, as compared to the Random sequences.[1] As shown in Fig. 2, RTs during late blocks were indeed faster for objects in Consistent (Fixed, X1, and X2 collapsed) sequences, relative to Random sequences. A repeated measures ANOVA revealed main effects of Sequence Type (Consistent vs. Random; $F_{1.39,\ 26.41} = 43.24$ $p < 0.0001$) and Serial Position within an object sequence ($F_{2.25,\ 42.71} = 17.91$ $p < 0.0001$). We also found a significant Study Block (Early vs. Late) by Serial Position interaction ($F_{2.95,\ 56.07} = 5.43$, $p < 0.003$) and a significant Sequence Type by Serial Position interaction ($F_{4,40,\ 83.60} = 2.95$, $p < 0.05$), all of which pointed to the fact that reaction times for objects in Consistent and Random sequences diverged from each other over the course of learning[2]. Overall accuracy was very high across

[1] We expected equally slow reaction times for position 1 across all sequences, because participants could not predict items in the current sequence until after the first item was presented.

[2] Overlapping (X1/X2) sequences and the non-overlapping (Fixed) sequence were combined to keep our behavioral analyses consistent with our EEG analyses. However, in late blocks position 4 RT is slower in X1/X2 sequences vs. position 4 in the Fixed sequence; $t(19) = 3.123$, $p = 0.0056$). We also find that for Consistent sequences in late blocks position 4 is slower than position 5 $t(19) = 2.24$, $p = 0.037$.

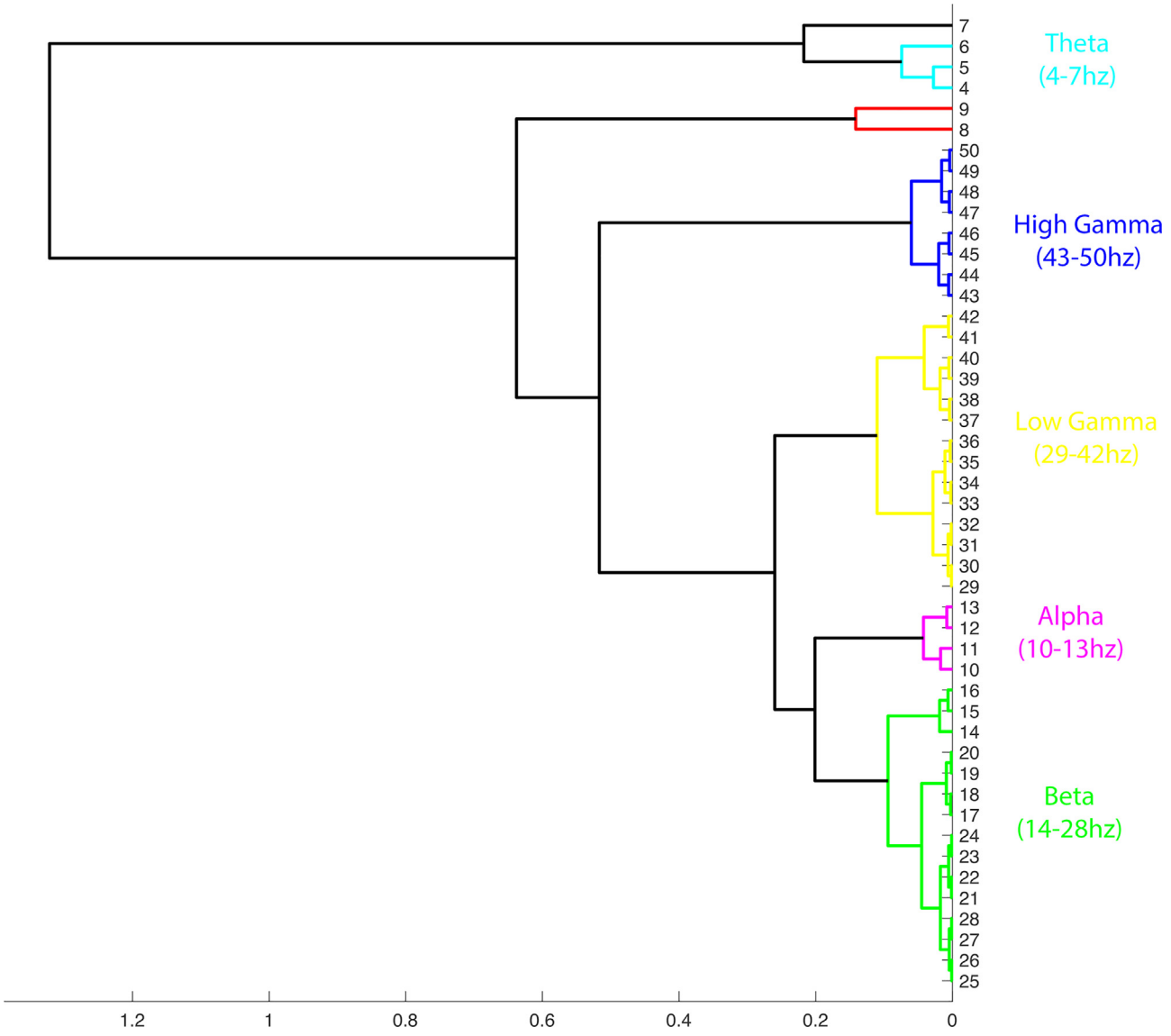

Fig. 1. Hierarchical clustering was used as a data driven method to derive frequency bands of interest for subsequent analysis. Clustering revealed bands that closely resembled canonical frequency bands (Theta, Alpha, Beta, Gamma).

blocks, positions, and sequences (~96%). To ensure any differences in reaction times to semantic questions were not driven by errors, we also analyzed error rates to semantic questions using a repeated measures ANOVA identical to the one used with reaction times. This analysis revealed no main effects or interactions, most likely due to subjects' near-ceiling performance. Taken together, these results demonstrate that participants were able use their sequence knowledge to predict upcoming objects in the Consistent sequences to facilitate their reaction times.

3.2. Theta oscillations associated with sequence learning

One of the goals of this study was to examine whether changes in theta oscillations accompanied learning of temporal relationships in object sequences. To this end, we contrasted activity in the theta band (4–7 Hz; see Methods) between Consistent and Random sequences across early (i.e., Blocks 1 and 2) and late blocks (i.e., Blocks 3 and 4). Our behavioral analysis suggests that participants were able to use their sequence knowledge to predict upcoming objects within Consistent sequences as compared to objects within the Random sequences. To examine oscillatory activity related to the prediction of upcoming items in the sequence, and to control for differences in response latencies between sequence types, we focused our analysis on response-locked, as opposed to stimulus-locked activity. These analyses focused on trials corresponding to positions 1–4 in each sequence. Position 5 was explicitly excluded because participants could not predict which object would come after the fifth object in an upcoming sequence. Oscillatory data were averaged across positions 1–4 and divided into early blocks (Blocks 1 and 2) and late blocks (Blocks 3 and 4). Results revealed decreased oscillatory power for trials in Consistent sequences, compared to Random sequences in late blocks vs. early blocks (4–7 Hz, 50 to 600 ms, $p < 0.05$) over frontal sensors (Fig. 3A). Follow-up tests indicated that these effects were driven by decreases in theta power for the Consistent sequences compared to the Random sequences in late blocks (4–7 Hz, −280 ms to 580 ms; $p = 0.0079$). This is in contrast to the early blocks, which showed no significant clusters between the Consistent and Random sequences in the theta band. These results demonstrate that, in late blocks, when participants show the biggest RT differences between Consistent and Random sequences, we also see significant frontal theta power differences between Consistent and Random sequences. This suggests that theta power decreases during learning could relate to improvements in sequence-based prediction of

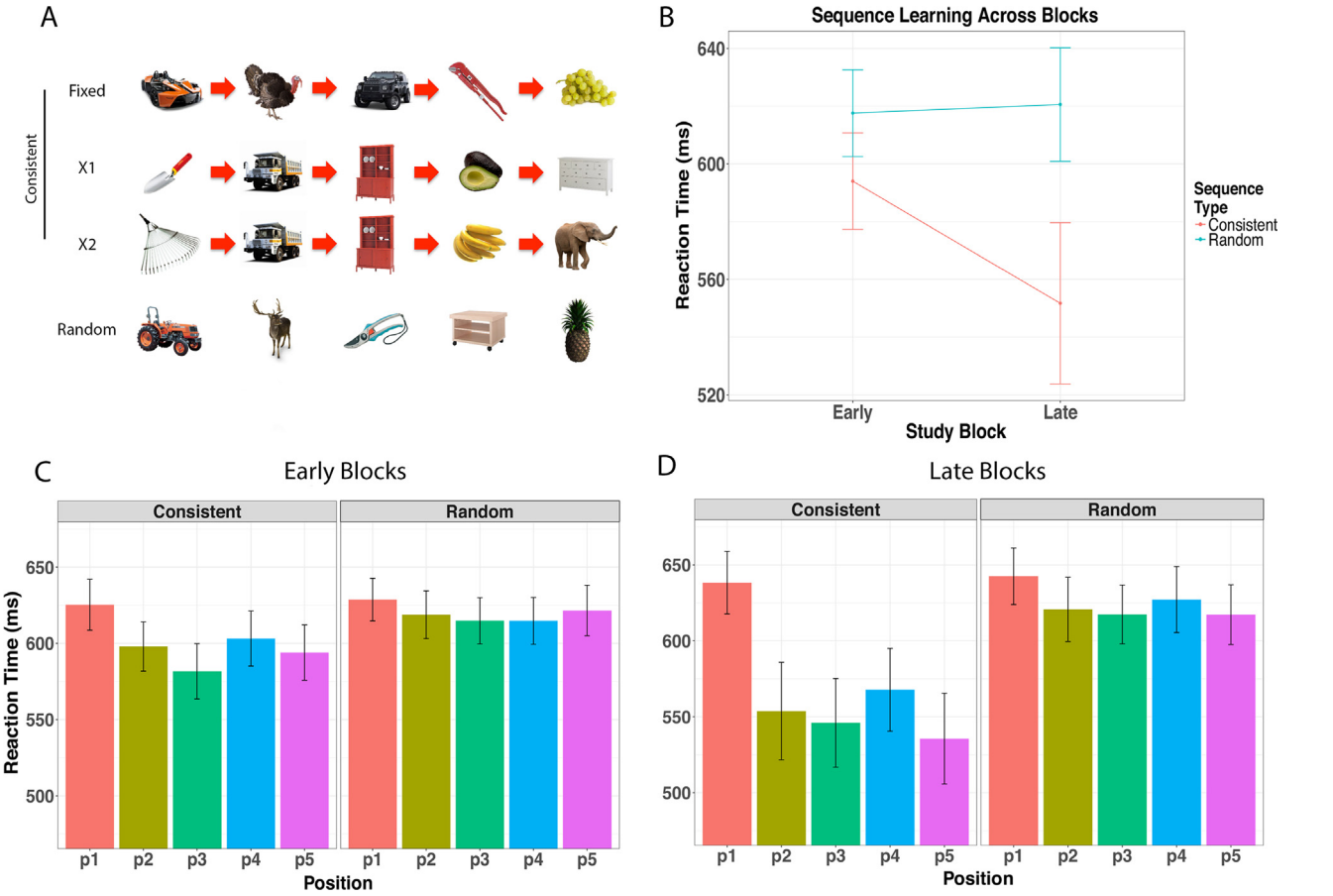

Fig. 2. Paradigm and Behavioral Results: (A) Example sequences presented to subjects. (B) Behavioral results from the sequence learning paradigm depicting average reaction time from positions 2–5 for the Consistent (Fixed, X1, and X2) and Random sequence types. Error bars denote ± standard error of the mean. (C) Reaction time by position in early blocks (blocks 1 and 2) for Consistent and Random sequences. Error bars denote ± standard error of the mean. (D) Same as C except late blocks (blocks 3 and 4).

upcoming stimuli.

3.3. Learning-related frontal theta increases at sequence boundaries

As noted above, participants could learn to predict upcoming objects within Consistent sequences, but they should be unable to predict the object to be presented immediately after the last item in the sequence (i.e., immediately after a sequence boundary). If theta power is inversely related to prediction of upcoming items, we would expect to see higher theta power following position 5, as compared with position 4, in the Consistent sequences. Furthermore, if this effect is related to learning about temporal relationships we should see changes across learning blocks. In line with this prediction, we found a significant increase in post-response theta power (4–7 Hz, 50–600 ms, $p = 0.045$) in position 5 compared to position 4 in late vs. early blocks for Consistent sequences (Fig. 4a). We then examined early and late blocks separately, to determine if the effect was driven by differences in only some of the learning blocks. Results revealed no significant differences between position 5 and position 4 in early or late blocks. These results demonstrate that over the course of learning theta power increases at the end of the sequence relative to other intra-sequence positions (position 4). Given the 5-item structure of the task it is possible that theta power increases may signal the formation of an event boundary.

3.4. Theta power predicts reaction time for upcoming objects in Consistent sequences

Our data indicate that theta activity elicited during processing of items in Consistent sequences decreases over the course of learning. As noted earlier, there is considerable evidence suggesting that frontal theta power is linked to prediction and prediction error-driven learning (e.g., Cavanagh et al., 2009; Cavanagh, Frank, Klein, & Allen, 2010; Cavanagh & Frank, 2014). In the context of our experiment, it is possible that post-response theta activity reflected the degree to which participants could predict subsequent items in a sequence. To test this hypothesis, we tested whether, on a trial-by-trial level, post-response theta activity was predictive of reaction times for subsequent items in Consistent sequences.

We used a linear mixed effects model with maximal random effects structure to examine this hypothesis (Barr et al., 2014). A linear mixed effects model was used to account for the nested structure of the dataset, allowing us to statistically model errors in our model clustered around individuals and trial types that violate the assumptions of standard multiple regression models. This allowed us to look at single-trial theta power and examine its relationship with participants' reaction time on semantic questions for upcoming objects. Single-trial theta power associated with objects in the Consistent sequences during late blocks was obtained by extracting band specific values from the significant electrodes and time windows as identified in the above analyses. These values were then averaged to obtain a single power value for each trial. We also included trial-specific Beta and Alpha band power identified in our power analyses (see alpha/beta section below) as control frequencies. For a given trial ($Trial_N$), power was extracted in each band along with the subsequent trial's ($Trial_{N+1}$) reaction time. Results revealed a significant effect of theta power on $Trial_N$ with RT on $Trial_{N+1}$ ($\beta = 4.585$; $F(1,11.184) = 10.59$, $p < 0.001$; Fig. 5a). In

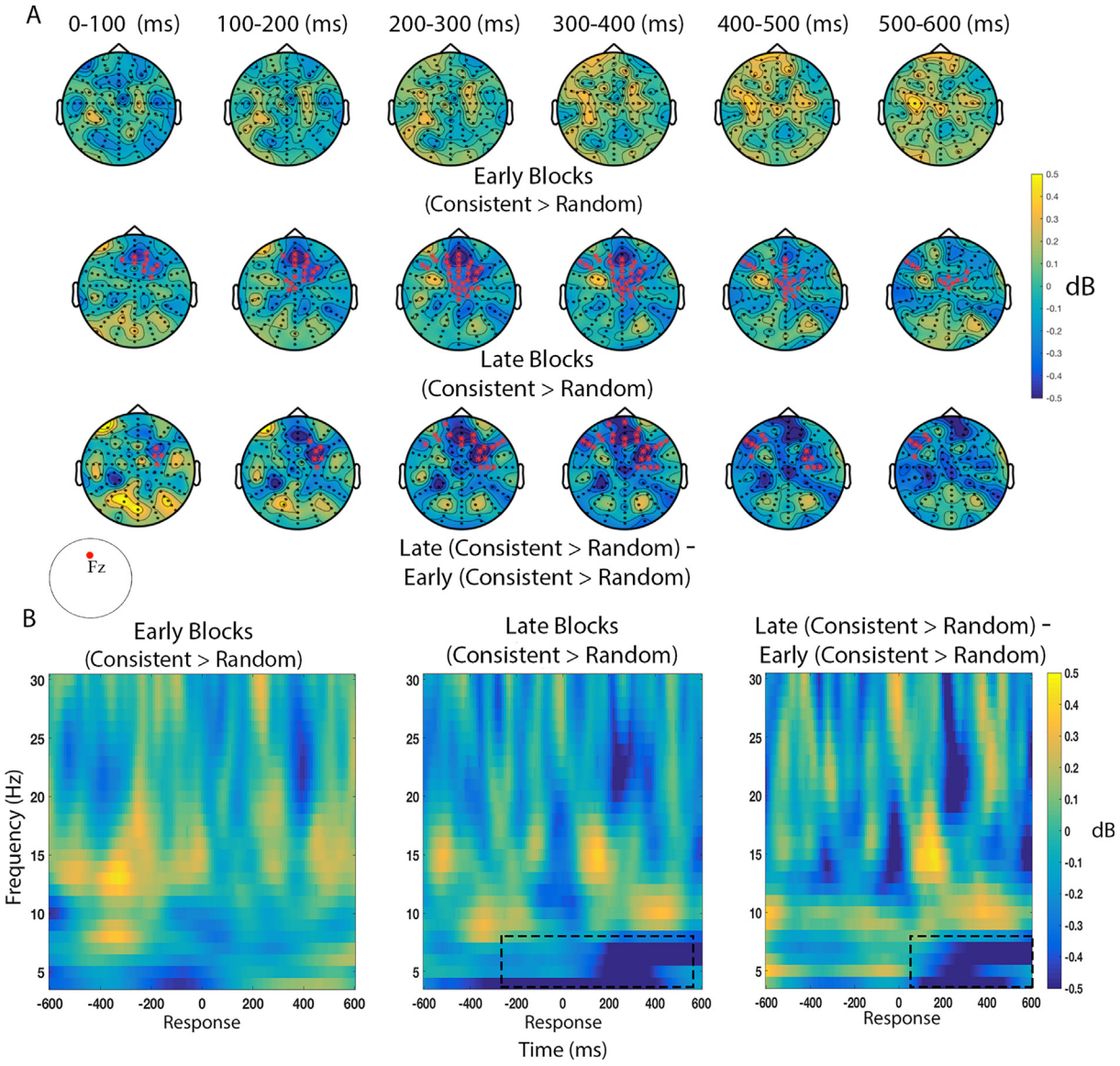

Fig. 3. Frontal Peri-Response Theta Power Changes over the Course of Sequence Learning: (A) Topographical maps depict scalp distribution of theta (4–7 Hz) power in 100 ms epochs following each response to items in positions 1–4. Highlighted electrodes denote significant electrodes. Top row - Topographic map of the difference in oscillatory power between Consistent > Random in early blocks. Middle row – same as top row except Consistent > Random in late blocks. Bottom row – same as middle and top row except (Consistent > Random late blocks) > (Consistent > Random late blocks) (B) Spectrograms from a representative electrode Fz. Left panel – Consistent > Random early blocks. Middle panel – Consistent > Random late blocks. Right panel – (Consistent > Random late blocks) – (Consistent > Random early blocks). Dashed box depicts significant time points in time–frequency space.

other words, theta power at the current trial predicted behavioral performance for the upcoming trial. Importantly, activity in other frequency bands were not predictive of behavioral response for the upcoming trial (Beta (14–28 Hz), $\beta = -3.358$, $F(1, 38.11) = 1.35$, $p = 0.16$; Alpha (10–13 Hz), $\beta = -1.996$, $F(1, 35.59) = 1.33$, $p = 0.18$; Fig. 5b and c). Collectively, these results suggest a special role for theta power in facilitating the behavioral predictions for upcoming events.

3.5. Alpha/beta oscillations associated with sequence learning

Our next sets of analyses sought to evaluate the contributions of alpha and beta oscillations in sequence learning. Mirroring the analysis pipeline for our theta analyses oscillatory data were averaged across positions 1–4 and divided into early blocks (Blocks 1 and 2) and late blocks (Blocks 3 and 4). Results revealed no significant differences in oscillatory power for trials in Consistent sequences, compared to Random sequences in late blocks vs. early blocks for either frequency band. To determine if alpha and beta power was stable across learning blocks, we examined early and late blocks separately. This revealed, increased oscillatory beta and alpha power for trials in Consistent sequences compared to Random sequences in late blocks but not early blocks, over parietal/occipital sensors (Beta (14–28 Hz, −520 ms to −80 ms, $p = 0.014$) and Alpha (10–13 Hz, −460 to −120 ms, $p = 0.006$; Fig. 6). Thus, in contrast to the post-response theta effects observed in our previous analyses, alpha/beta power increased over the course of learning, and learning-related modulations preceded behavioral responses.

3.6. Beta/alpha power on current trial predict reaction time for objects in Consistent sequences

In contrast to our analyses of theta power, beta and alpha power on the current trial was not predictive of participants' reaction times on the

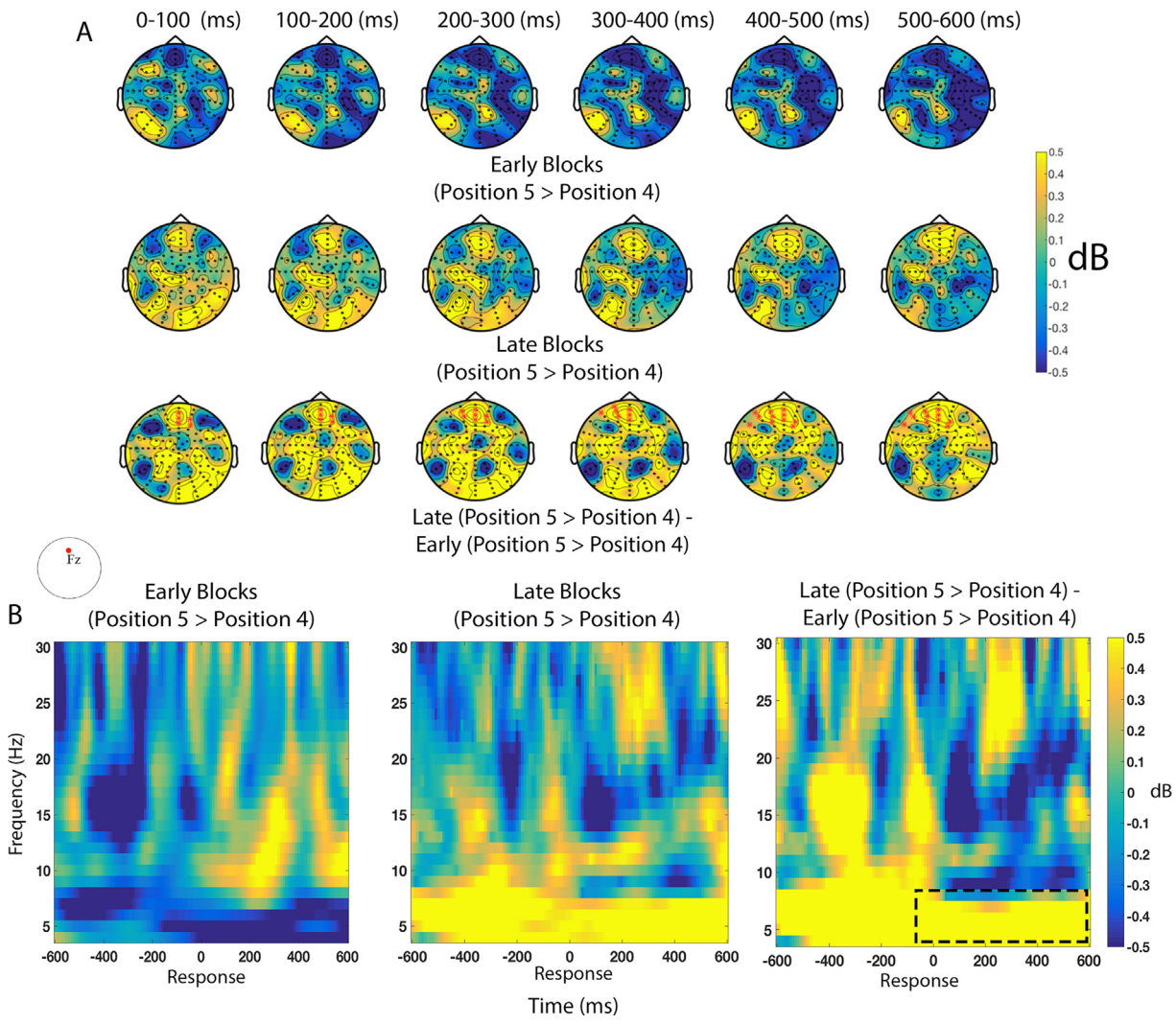

Fig. 4. Learning Related Frontal Theta Increases at Sequence Boundaries: (A) Topographical distributions of theta (4–7 Hz) power in 100 ms epochs following each response to items in positions 4 and 5. Highlighted electrodes denote significant electrodes. Top row - Topographic map of the difference in oscillatory power between position 5 > position 4 for Consistent sequences in early blocks. Middle row – same as top row except position 5 > position 4 for Consistent sequences in late blocks. Bottom row – same as middle row except (position 5 > position 4 late blocks) > (position 5 > position 4 early blocks) for Consistent sequences. (B) Spectrograms from a representative electrode Fz. Left panel – position 5 > position 4 for Consistent sequences in early blocks. Middle panel – position 5 > position 4 for Consistent sequences in late blocks. Right panel – (position 5 > position 4 late blocks) > (position 5 > position 4 early blocks). Dashed box depicts significant time points in time-frequency space.

next trial in Consistent sequences (Beta (14–28 Hz), $\beta = -3.358$, F(1, 38.11) = 1.35, p = 0.16; Alpha (10–13 Hz), $\beta = -1.996$, F(1, 35.59) = 1.33, p = 0.18; Fig. 5b and c). Given that the timing of these effects preceded behavioral responses, we reasoned that beta and alpha power could contribute to the speeding of participant's reaction time on the current trial. To further investigate the role of alpha and beta oscillations in facilitating behavioral outcomes, we examined the relationship between pre-response alpha/beta on reaction time for the current trial. To this end, using the significant spatio-temporal clusters identified above to extract single-trial alpha and beta power. These values were then averaged to obtain a single power value for each trial and inputted into a mixed effects model with a maximal random effects structure, as described in the theta analyses (see also Methods). Results revealed a significant effect of beta and alpha power on the current trial with reaction time on the current trial (Beta, $\beta = -17.664$, F(1, 22.11) = 27.03, $p = 3.21 \times 10^{-5}$; Alpha, $\beta = -4.576$, F(1,21.17) = 5.63, p = 0.034, Fig. 7). These results demonstrate that alpha/beta oscillations occurring before a response could facilitate processing of items in Consistent sequences, thereby resulting in faster reaction time.

4. Discussion

The present study examined changes in oscillatory power over the course of sequence learning. We found that post-response oscillatory power in the theta band declined over the course of sequence learning. In late, but not early blocks, theta power was lower for items in Consistent sequences than for items in Random sequences (Fig. 3). Crucially, we found that band-specific decreases in oscillatory theta power were significantly correlated with reaction times for upcoming semantic decisions in Consistent sequences (Fig. 5). These results suggest a relationship between theta activity and the ability to use sequence knowledge to predict upcoming events. We also found increased beta and alpha power for Consistent sequences compared to Random sequences in late blocks over parietal and occipital electrodes (Fig. 6). Unlike theta activity, learning-related activity in the beta and alpha bands was increased during the pre-response period, and these enhancements were correlated with reaction time on the current trial, rather than the subsequent trial (Fig. 7). These findings indicate different roles for theta and alpha/beta oscillations in sequence learning and representation.

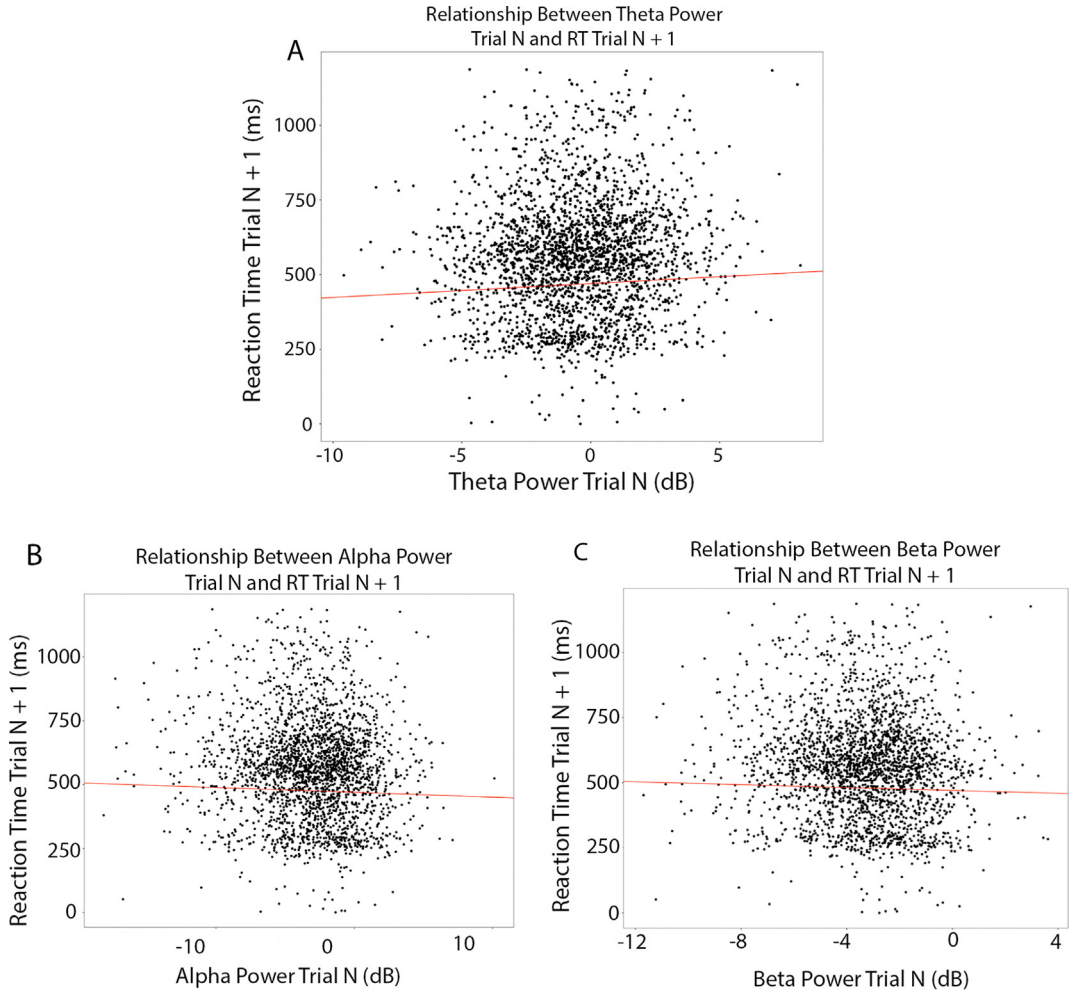

Fig. 5. Post-response theta power uniquely predicts RT facilitation on the next trial. (A) Scatter plot of theta power on trial N versus reaction time on N + 1. Red line denotes fixed effects from the statistical model. (B) Same as A except using beta on current trial (C) Same as A except using alpha on current trial. Note models are fit to Consistent sequences in late blocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Theta effects

Several scalp EEG studies have linked frontal midline theta in humans to a variety of memory related processes including episodic memory encoding (Klimesch, 1999; Long et al., 2014; Sederberg et al., 2003) and retrieval (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Jacobs, Hwang, Curran, & Kahana, 2006; Meyer, Grigutsch, Schmuck, Gaston, & Friederici, 2015), prediction (Cavanagh & Frank, 2014; Cavanagh et al., 2009, 2010), and working memory maintenance (Gevins et al., 1997; Hsieh et al., 2011; Jensen & Tesche, 2002). Cavanagh & Frank argued that prediction error could serve as a generalized mechanism for reinforcing behaviorally-relevant predictions. In the current study, the structured order of the Consistent sequences allow participants to form predictions about upcoming items in the sequence. Consistent with Cavanaugh & Frank's (Cavanagh & Frank, 2014) model, we found that theta power was high when participants were initially learning to predict upcoming objects, and it declined as they became proficient at anticipating upcoming objects.

Results from Clarke et al. (2017), converge with the present results to suggest a role for theta activity in learning and prediction. Clarke and colleagues used an associative learning paradigm to evaluate the role of neural oscillations over the course of learning. In this paradigm, participants saw an object, and after a delay, they made a button press and received immediate feedback as to the accuracy of the response. Across repetitions, subjects learned the associations and were able to plan responses during the delay period. Clarke et al. found that, frontal midline theta power was high early in learning, and theta power gradually decreased as associations were learned. Additionally, Clarke et al. found that posterior alpha and beta oscillations that increase as associations become well-learned. These data provide evidence that theta oscillations might be important for the initial learning of cross-temporal associations, and that theta power as these associations are mastered. Integrating our findings with those of Clarke et al. (2017), it is likely that learning-related theta modulations are not specific to sequence learning. Instead, they might more generally promote learning of cross-temporal contingencies in a number of tasks that benefit from prediction (Brincat & Miller, 2015; Fuster & Bressler, 2012).

Given the frontal topography of the effects observed, it is unlikely that our effects could be driven solely by volume-conducted theta activity generated in the hippocampus. Theta activity in anterior cingulate cortex (ACC) and medial prefrontal cortex (PFC), however, could likely drive theta oscillations in scalp recordings consistent with those observed in the current study (Cohen, 2011; Gilboa and Moscovitch, 2016; Onton, Delorme, & Makeig, 2005; Raghavachari et al., 2001). Further support for this idea comes from studies in monkeys showing that the dorsolateral and medial prefrontal cortices contribute to the generation of frontal midline theta (Tsujimoto, Shimazu, & Isomura, 2006). In addition to power changes, it is important to consider the possibility that scalp-recorded theta might reflect changes in theta coherence (i.e., synchrony) across local neural populations or between different brain regions. Relevant to this point, studies in rodents (Buzsáki, 2002) and humans (Ekstrom et al., 2005; Lega, Jacobs, &

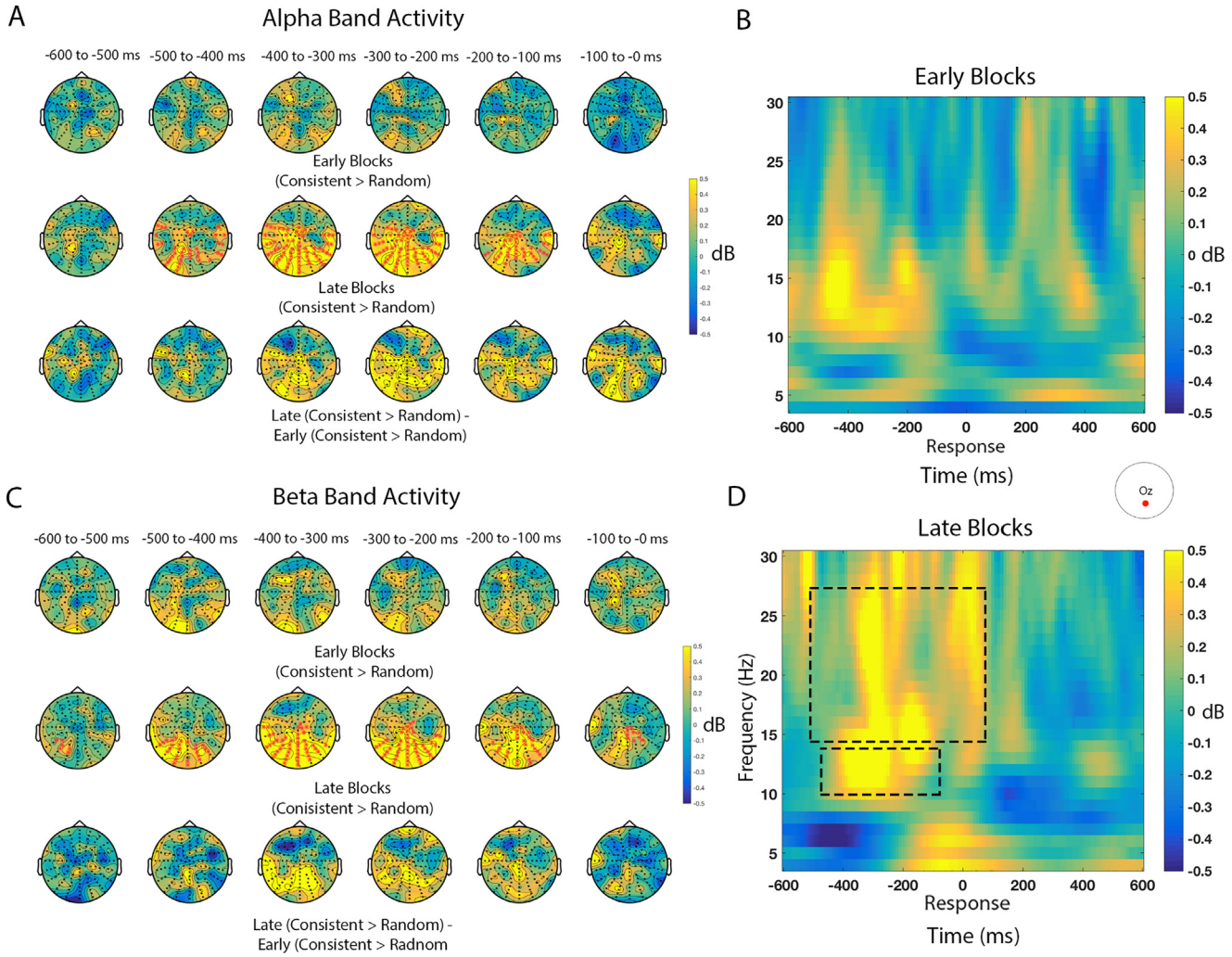

Fig. 6. EEG results for alpha and beta bands. (A) Topographical distributions of alpha (10–13 Hz) power in 100 ms epochs preceding each response to items in positions 1–4. Highlighted electrodes denote significant electrodes. Top row - Topographic map of the difference in oscillatory power between Consistent > Random late in early blocks. Middle row – same as top row except Consistent > Random in late blocks. Bottom row – same as middle row except (Consistent > Random late blocks) > (Consistent > Random early blocks). (B) Spectrograms from a representative electrode Oz. Consistent > Random early blocks. (C) Same as A except Beta (14–28 Hz) power pre-response. (D) Same as B except Consistent > Random late blocks. Dashed boxes depict significant time points in time-frequency space.

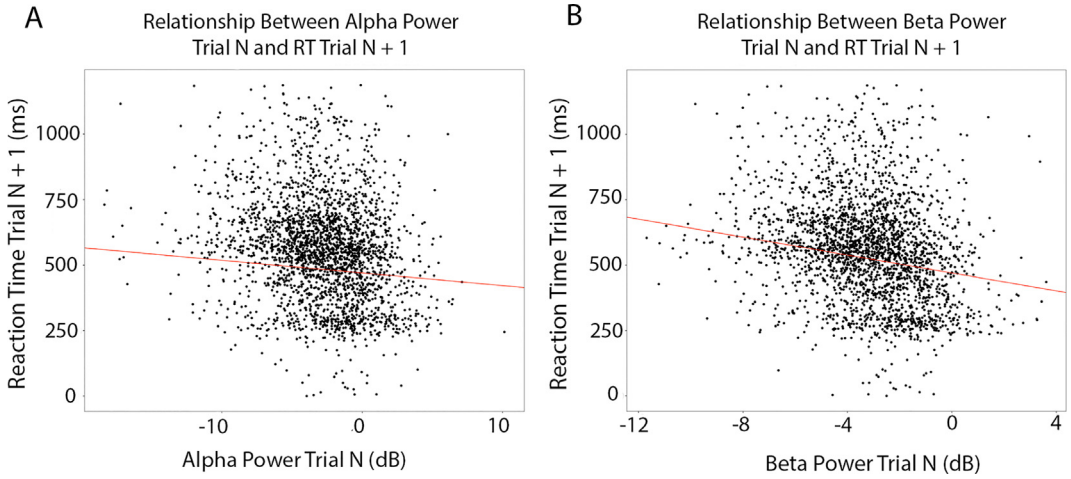

Fig. 7. Pre-response alpha and beta power uniquely predict RT facilitation on the current trial. (A) Scatter plot of Alpha power on trial N versus reaction time on trial N. Red line denotes fixed effects from the statistical model. (B) Same as A except using beta on current trial. Note models are fit to Consistent sequences in late blocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Kahana, 2012; Long et al., 2014) have shown that theta oscillations are present in the hippocampus, and evidence suggests that theta coherence might be a mechanism for coordinating activity between the hippocampus and PFC (Backus, Schoffelen, Szebényi, Hanslmayr, & Doeller, 2016; Jones, Wilson, Tsien, Tonegawa, & Wilson, 2005; Siapas, Lubenov, & Wilson, 2005).

Recent work from Brincat and Miller (2015) provides a potential account for how response-related theta band synchrony might influence interactions between the hippocampus and PFC. Brincat et al. simultaneously recorded activity from neurons in the monkey hippocampus and dorsolateral PFC as monkeys learned pair associations between temporally-separated objects. During initial learning of associations, post-response phase-synchronization between oscillations in hippocampus and PFC was higher on incorrect trials (i.e., when the animal could not predict the upcoming object to select) than on correct trials. Error-related theta synchrony between hippocampus and PFC declined over the course of learning, whereas alpha/beta band synchrony increased over the course of learning. In the present study, we cannot say that theta activity observed was driven by error feedback, as participants performed the incidental semantic decision task with high accuracy. That said, our findings parallel those of Brincat and Miller (2015), in that, early in learning, participants could not form accurate predictions about upcoming items in both Consistent and Random sequences. Thus, it is reasonable to think that post-response theta activity reflected an inability to predict the next item (i.e., a prediction error). However, as sequence learning progressed in late blocks, participants were more likely to make correct predictions for upcoming items in Learned sequences. In contrast, temporal relationships changed on each iteration of the Random sequences, and thus post-response theta was significantly higher for Random, relative to Consistent sequences during late blocks.

In the present study, we manipulated sequence structure such that participants learned to anticipate upcoming objects in learned sequences. Because temporal relationships were constant for the Consistent sequences, prediction error would be expected to be high early in learning and low late in learning. It is possible, however, that theta might differentially relate to learning when one cannot predict upcoming events versus when one makes an incorrect prediction about a subsequent event. These factors could be disentangled in a future study in which participants learn probabilistic, rather than deterministic, relationships between items. With a probabilistic sequence-learning paradigm, one could differentiate between post-response theta related to learning of sequential relationships and post-response theta following violations of learned sequence relationships (see, for example, Allen, Morris, Mattfeld, Stark, & Fortin, 2014).

4.2. Alpha/beta effects

In addition to the observed decrease in post-response theta power, we also observed pre-response increases in Alpha/Beta power for Consistent sequences relative to Random sequences that evolved over the course of learning. Consistent with this finding, the aforementioned study by Clarke and colleagues revealed enhancements in alpha and beta power over the course of associative learning, and Brincat and Miller (2015) found that alpha/beta synchrony between hippocampus and PFC increased over the course of learning. Although the functional significance of learning-related changes in alpha and beta oscillations is unclear, the existing literature suggests possible interpretations.

Beta oscillations in primary motor cortex and sensorimotor cortex have been observed in relation to motor behavior in humans (Jenkinson & Brown, 2011; Pfurtscheller & Lopes da Silva, 1999; Salenius & Hari, 2003). Specifically, studies have shown that synchronized beta oscillations are related to movement preparation in monkeys (Donoghue, Sanes, Hatsopoulos, & Gaál, 1998; MacKay & Mendonça, 1995; Sanes & Donoghue, 1993). The timing of the alpha/beta effects observed was pre-response suggesting that alpha/beta synchronizations before an action could be related to response preparation. Consistent with this idea, our data show that the up-regulation of these oscillations is correlated with improved behavioral performance (see also Androulidakis et al., 2007).

An alternative hypothesis could be that beta oscillations are important for representing the existing state of affairs or recent past. Engel and Fries (2010) hypothesized that beta band activity should be higher if the sensorimotor system has to actively maintain a cognitive set. Empirical evidence from Morton and Polyn (2017) has provided support for this idea. Using a multivariate pattern classification approach, they found that the pattern of beta band activity over posterior electrodes reflected the category of recently presented stimuli and that classification performance for stimulus category decreased gradually as the category changed. Our results are consistent with the notion that beta band activity is involved in representing the recent past. Over the course of learning participants form associations between items in the Consistent sequences creating a “cognitive set” for these sequences. Thus, it is possible that the increased oscillatory beta power in our task reflects greater maintenance of a cognitive set for the Consistent compared to the Random sequences.

Alpha band oscillations have long been interpreted as “cortical idling” (Pfurtscheller, Stancák, & Neuper, 1996) or attributed to the filtering of task-irrelevant information (Jensen & Mazaheri, 2010). However, there is growing evidence that posterior alpha oscillations are important for the maintenance of items in working memory (Hsieh et al., 2011; Jensen & Tesche, 2002; Schack & Klimesch, 2002) and are modulated by expectation (Mayer, Schwiedrzik, Wibral, Singer, & Melloni, 2016; Rohenkohl & Nobre, 2011; Samaha et al., 2017; Samaha, Bauer, Cimaroli, & Postle, 2015). Work from Mayer and colleagues found that pre-stimulus alpha oscillations are related to predictions about the visibility of an upcoming letter in a sequence. Interestingly, they found that the spatial topography of alpha power during the pre-stimulus period was highly overlapping with topography after stimulus onset, suggesting a role for alpha oscillations in forming top-down sensory predictions and comparing them to a perceived stimulus. Relating their findings to our current results, it is possible that the differences in alpha power between Consistent and Random sequences in late learning blocks might be related to predictions of upcoming visual stimuli.

4.3. Conclusion

In conclusion, our results highlight the qualitative distinctions between frontal theta and posterior alpha/beta oscillations in the context of sequence learning, with theta and alpha/beta activity preferentially relating to future and current events, respectively. The current work converges nicely with neurophysiological studies implicating these oscillations in synchronization of learning-related activity in the hippocampus and prefrontal cortex (Benchenane et al., 2010; Brincat & Miller, 2015; Place, Farovik, Brockmann, & Eichenbaum, 2016; Siapas et al., 2005). Future studies could build on these findings by investigating how prefrontal-hippocampal synchrony affects learning-related oscillations in the theta, alpha, and beta bands. Our results provide direction to future work investigating whether these rhythms can be modulated using stimulation techniques to improve behavioral outcomes. By selectively inhibiting or enhancing specific rhythms, we can begin to better understand the complex relationship oscillations play in the acquisition and subsequent deployment of learned information.

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